UNIVERSIDADE FEDERAL DO PARANÁ

LUISA FERNANDA LIÉVANO LATORRE

DETERMINANTES DA SOBREPOSIÇÃO DE INTERAÇÕES EM REDES NEOTROPICAIS DE POLINIZAÇÃO MORCEGO-PLANTA

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Dissertação apresentada ao curso de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas, Universidade Federal do Paraná, como requisito parcial à obtenção do título de mestre em Ecologia e Conservação.

Orientadora: Profa. Dra. Isabela Galarda Varassin

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"Sólo el murciélago
Se entiende con el mundo,
Pero al revés"

(Mario Benedetti)

RESUMO

As comunidades ecológicas estão compostas por espécies que podem compartilhar recursos semelhantes, gerando sobreposição de nicho. Um destes recursos são os polinizadores e o néctar das plantas. Neste caso, a sobreposição de nicho é o grau de compartilhamento de parceiros entre espécies de uma mesma guilda. A sobreposição de nicho pode ser afetada por diferentes fatores ambientais e biológicos, diminuindo com uma maior sazonalidade climática, riqueza taxonômica e diversidade filogenética e funcional. O papel desses fatores como determinantes da sobreposição de nicho tem sido estudado mediante uma abordagem de redes complexas, usando como modelo as aves e insetos. Porém, no caso dos polinizadores vertebrados neotropicais, não é possível assumir que os determinantes encontrados em beija-flores sejam semelhantes para os morcegos. Neste contexto, o objetivo do trabalho é identificar os determinantes da sobreposição de nicho nas redes neotropicais de polinização morcego-planta. Para isso, utilizaram-se 22 redes de interação (12 ponderadas e 22 binárias) distribuídas entre o norte do México e sul do Brasil. A sobreposição de nicho foi descrita usando a especialização complementar média ($<d'>$) para as redes ponderadas e o Índice de Morisita-Horn ($\hat{C}_H$) para as binárias. Estas variáveis foram relacionadas com a sazonalidade climática, riqueza da guilda, diversidade filogenética e funcional para as duas guildas através de modelos lineares. As comunidades com menor riqueza de plantas e localizadas em regiões com maior sazonalidade da precipitação exibiram menor sobreposição de nicho, enquanto que comunidades com baixa diversidade filogenética de morcegos apresentaram maior sobreposição de nicho. A relação entre a sobreposição de nicho, sazonalidade da precipitação e diversidade filogenética era esperada porque uma maior sazonalidade modifica as fenologias de plantas e polinizadores, causando a formação de módulos temporais de floração, enquanto que espécies com histórias evolutivas diferentes tendem a explorar diferentes recursos. Porém, ainda que não esperávamos a relação negativa entre sobreposição de nicho e riqueza de plantas, esta pode ser resultado da tendência de comunidades com mais recursos apresentarem interações mais generalistas, permitindo que todos os recursos sejam acessados dentro da comunidade. Estes resultados se diferenciam do encontrado para interações de beija-flor-planta, que tendem a ser mais especializadas em ambientes com alta precipitação e maior riqueza de espécies. Finalmente, este estudo reforça a importância da sazonalidade climática, a riqueza de espécies e a diversidade filogenética na sobreposição de nicho em redes de interação mutualística, além de evidenciar as diferenças entre grupos de polinizadores.

Palavras chave: Chiroptera, diversidade filogenética, diversidade funcional, macroecologia, polinização, redes de interação.

ABSTRACT

Ecological communities are composed by species that could share similar resources, causing niche overlap. One of those resources are pollinators or plants' nectar. In this case, niche overlap is the degree of partner sharing among species on a same guild. Niche overlap may be affected by different environmental and biological factors, decreasing with higher climate seasonality, species richness and phylogenetic and functional diversity. The role of these factors as niche overlap's drivers has been intensely studied for birds and insects using a complex network approach. However, we cannot assume that hummingbirds' drivers are the same than bats' drivers for Neotropical vertebrate pollinators. In this context, our aim is to identify the drivers of niche overlap in bat-plant Neotropical pollination networks. For that, we used 22 interaction networks (12 weighted and 22 binary networks) located between North of Mexico and South of Brazil. Niche overlap was described using the mean complementary specialization ($<d'>$) for weighted networks and Morisita-Horn Index ($\hat{C}_H$) for binary ones. We related niche overlap with climate seasonality, guild richness, phylogenetic and functional diversity for each guild through linear models. We found that communities with lower plant richness and in regions with higher precipitation seasonality have a lower niche overlap, as well as communities with lower bat phylogenetic diversity have a higher niche overlap. The relationship between niche overlap, precipitation seasonality, and phylogenetic diversity was expected because a higher seasonality modifies plant and pollinator phenologies, causing the formation of temporal flowering modules, while species with different evolutionary histories tend to explore different resources. However, though the negative relationship between niche overlap and plant richness was not expected, it could occur because communities with higher resource availability tend to have species with more generalized interactions, that allow them to access all resources. Also, our results are different from the patterns found for hummingbird-plant interactions which tend to be more specialized in rainy environments and with higher species richness. Finally, this study reinforces the importance of climate seasonality, species richness, and phylogenetic diversity as main drivers of niche overlap in mutualistic interaction networks and also, highlights the differences between bat-plant and other pollination systems.

Key-words: Chiroptera, functional diversity, interaction networks, macroecology, pollination, phylogenetic diversity.

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INTRODUÇÃO GERAL

As comunidades biológicas estão compostas por diferentes espécies, que possuem diferentes requerimentos. O nicho ecológico reúne todos os fatores ambientais e biológicos necessários para a existência de uma espécie em um ambiente (HUTCHINSON, 1959). Isto implica que o nicho abrange as condições ambientais e as interações biológicas que limitam a existência de uma determinada espécie em uma comunidade (HUTCHINSON, 1959). É comum que duas ou mais espécies que coexistem compartilhem algum recurso (exemplo: alimento, polinizadores, abrigo, etc.). Porém, a presença das espécies é afetada quando esses recursos são limitados no ambiente. Este processo é conhecido como competição interespecífica (PETRANKA, 1989; TILMAN, 1990). Quando ocorre competição interespecífica, o nicho das espécies é menor do que o esperado se estas não coexistissem, chegando a extremos onde as espécies não podem coexistir em uma mesma comunidade (HARDIN, 1960; HUTCHINSON, 1959). Por outro lado, é possível encontrar comunidades nas que coexistem espécies que exploram recursos semelhantes. Em outras palavras, existe uma sobreposição do nicho dessas espécies (HURLBERT, 1978; PIANKA, 1973). O entendimento da sobreposição de nicho e dos mecanismos que permitem a coexistência das espécies é chave na ecologia, já que permite entender processos de especiação, montagem de comunidades e o papel da competição na evolução de espécies e interações ecológicas (GODOY; KRAFT; LEVINE, 2014). Entre estas interações, destaca-se a polinização, onde a competição por polinizadores parece ser uma força ecológica e evolutiva básica na evolução das plantas (ARMBRUSTER, 2017). A sobreposição de nicho está ligada ao conceito de especialização (OLLERTON et al., 2007), embora que existam diferentes maneiras de definir como uma espécie é especialista. No caso das interações mutualísticas como a polinização, a especialização pode ser descrita pelo número de espécies com as quais uma planta ou polinizador interage (especialização ecológica), a diversidade de grupos funcionais de parceiros mutualísticos, como por exemplo, flores polinizadas por aves (especialização funcional), adaptações morfológicas e funcionais para atrair/visitar certos parceiros (especialização fenotípica, ex.: comprimento da corola e produção de néctar de uma flor) e finalmente, o processo evolutivo que derivou na especialização da interação (especialização evolutiva) (OLLERTON et al., 2007). A especialização também pode ser descrita ao nível de comunidade, onde espécies de uma mesma guilda (grupo de espécies que exploram o

mesmo recurso) com um alto grau de especialização ecológica geram uma baixa sobreposição de nicho, porque o compartilhamento de parceiros mutualísticos é baixo (BORCHERT, 1998). Por conseguinte, já que as interações fazem parte do nicho das espécies e o estudo da especialização ecológica nas comunidades fornece informação sobre o uso do recurso (interações) pelas diferentes espécies da comunidade (ARMBRUSTER, 2017; FENSTER et al., 2004; OLLERTON et al., 2007), é possível avaliar a sobreposição de nicho mediante a sobreposição/especialização das interações mutualísticas. Neste estudo usaremos o termo sobreposição de nicho para referirmos ao grau de compartilhamento de interações entre polinizadores e plantas. Atualmente, a abordagem de redes complexas tem sido amplamente utilizada para estudar as interações mutualísticas ao nível de comunidade. Esta abordagem fornece vantagens ao avaliar a comunidade como um todo e não só suas partes, permitindo encontrar propriedades emergentes que seriam ignoradas ao estudar os componentes separadamente (BASCOMPTE; JORDANO, 2007). Ainda que as métricas de rede não avaliem exatamente a especialização ecológica (sensu OLLERTON et al. 2007), estas permitem avaliar a distribuição das interações ao nível da comunidade para descrever a especialização das interações. Consequentemente, os estudos com redes de interação têm contribuído ao entendimento da especialização das interações nas comunidades e seus determinantes, tanto em escala local como regional (ARMBRUSTER, 2017). Alguns dos determinantes da sobreposição de nicho em interações mutualísticas e em maiores escalas são: (1) fatores ambientais como a sazonalidade climática, e (2) fatores biológicos das redes, como a riqueza e a diversidade filogenética ou funcional (DALSGAARD et al., 2011, 2017; MARTÍN-GONZÁLEZ et al., 2015; MARUYAMA et al., in press; OLESEN; JORDANO, 2002; SCHLEUNING et al., 2012, 2014; SEBASTIÁN-GONZÁLEZ et al., 2015; ZANATA et al., 2017). Os estudos citados focaram em certos grupos de polinizadores, mas os determinantes da sobreposição de nicho permanecem incertos para outros.

Os morcegos (Chiroptera: Mammalia) polinizam em torno de 250 gêneros de plantas tropicais, as quais são beneficiadas com uma dispersão a longas distâncias do seu pólen, devido à capacidade de voo dos morcegos (FLEMING; GEISELMAN; KRESS, 2009; FLEMING; MUCHHALA, 2008). Os morcegos nectarívoros estão presentes nos trópicos, divididos em morcegos do Velho Mundo (família Pteropodidae) e do Novo Mundo (família Phyllostomidae). Os morcegos nectarívoros neotropicais polinizam espécies pertencentes a

pelo menos 43 famílias e 89 gêneros de plantas vasculares, sendo as principais famílias Acanthaceae, Agavaceae, Bignoniaceae, Bromeliaceae, Capparaceae, Cactaceae, Fabaceae, Gesneriaceae, Malvaceae, Myrtaceae e Solanaceae (FLEMING; MUCHHALA, 2008). A família Phyllostomidae possui a maior diversidade de morcegos neotropicais, os quais estão adaptados a diferentes tipos de dietas, entre as que está a nectarivoria. Os morcegos adaptados a se alimentar obrigatoriamente de néctar estão agrupados nas subfamílias Glossophaginae e Lonchophyllinae, mas também existem morcegos que podem se alimentar de néctar facultativamente, como as espécies pertencentes às subfamílias Carolliinae, Stenodermatinae e Phyllostominae (DATZMANN; VON HELVERSEN; MAYER, 2010). Os nectarívoros obrigatórios desenvolveram diferentes adaptações morfológicas que lhes permitem acessar diferentes tipos de flores e sobreviver com uma dieta baseada em néctar, sendo que o grau de desenvolvimento dessas características parece estar associado com os recursos utilizados por essas espécies (BOLZAN et al., 2015; FLEMING; GEISELMAN; KRESS, 2009).

Os determinantes da sobreposição de nicho em interações beija-flor–planta tem sido estudados anteriormente e sabemos que as interações nestes sistemas de polinização são afetadas pela precipitação, a riqueza, a diversidade funcional e filogenética das espécies presentes nas comunidades (DALSGAARD et al., 2011; MARTÍN-GONZÁLEZ et al., 2015; MARUYAMA et al., in press; ZANATA et al., 2017). Porém, devido às diferenças existentes entre morcegos e beija-flores, não é possível afirmar que as interações mutualísticas morcego-planta respondam aos mesmos fatores (MELLO et al., 2011). Portanto, este estudo procura entender quais são os determinantes ambientais e biológicos que atuam sobre a sobreposição de nicho nas interações morcego-planta, mediante uma abordagem de redes complexas em uma escala continental. Para isto, foi realizado um estudo com 22 comunidades de morcego-planta distribuídas no Neotrópico, avaliando a relação da especialização das interações com a sazonalidade climática, riqueza e diversidade filogenética e funcional. Os resultados do estudo são apresentados no Capítulo 1.

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CAPÍTULO 1

DRIVERS OF NICHE OVERLAP IN NEOTROPICAL BAT-PLANT POLLINATION NETWORKS

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Running title: Niche overlap in bat-plant networks

Title: Drivers of niche overlap in Neotropical bat-plant pollination networks

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Abstract

Aim: Communities are composed by species that share different resources. When resource is limited, niche overlap occurs. Interactions are an aspect of niche in pollination systems. Both the number of interactions and niche overlap in pollination networks are affected by environmental and biological factors, such as climate seasonality, species richness, functional and phylogenetic diversity. Vertebrates are important pollinators in Neotropics and the drivers of hummingbirds' niche overlap are known. However, drivers of niche overlap in bat-plant pollination networks must be different than hummingbirds ones. The aim of this study was to identify the drivers of niche overlap in Neotropical bat-plant pollination networks.

Location: Twenty-two forested and open ecosystems in the Neotropical region (31°43′N to 25°21′S).

Major taxa studied: Chiroptera; angiosperms

Methods: We measured the niche overlap of bats and plants, through species level complementary specialization, $<d'>$, and Morisita-Horn index, $\hat{C}_H$, on 22 bat-plant pollination networks (12 weighted and 22 binary). Using a model selection approach, we tested the effects of the following factors: temperature and precipitation seasonality, guild richness, functional and phylogenetic diversity on both plant and bat niche overlap.

Results: Plant niche overlap in weighted networks was lower in regions with increased precipitation seasonality and lower plant richness. On the other hand, bat niche overlap in binary networks was lower in communities with higher bat phylogenetic diversity.

Main conclusions: Precipitation seasonality, plant richness and bat phylogenetic diversity are the main drivers of niche overlap in Neotropical bat-plant pollination networks. Our results

expand the knowledge about niche overlap in vertebrate pollination systems and, reinforce the importance of climate seasonality as well as species richness on the niche overlap in mutualistic systems. Also, our study highlights the relevance to include species evolutionary history.

Key-words: Chiroptera, chiropterophily, climate seasonality, ecological specialization, functional diversity, interaction networks, macroecology, nectarivory, pollination, phylogenetic diversity.

INTRODUCTION

Biological communities are composed by species that use different resources. Niche encompasses both environmental and biological factors required for species occurrence in an area (Hutchinson, 1959). Hence, in a community where two or more species use the resources similarly, niche overlap between them occurs (Hurlbert, 1978; Pianka, 1973). In pollination systems, flowers and animals are resources for pollinators and plants, respectively, and resource overlap may occur within guilds in the community (Borchert, 1998). For that reason, we can use interaction specialization as an approximation to niche overlap in pollination communities. A way to assess interaction specialization and niche overlap is using the complex network approach (Armbruster, 2017; examples: Blüthgen, Menzel, & Blüthgen, 2006; Dalsgaard et al., 2011; Schleuning et al., 2012). Since this approach analyzes the community as a whole, it may reveal undetected emergent properties, such as interaction specialization, which is ignored when studying the community parts separately (Bascompte & Jordano, 2007). Since interactions are part of species niches, we use interaction specialization as an indicator of the niche overlap for each species included in our communities.

Patterns of niche overlap in mutualistic networks at large scales may change according to environmental factors, with climate factors being one of the most important drivers (Dalsgaard et al., 2011, 2017; Olesen & Jordano, 2002; Ollerton, 2006; Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009; Schleuning et al., 2012, 2014; Trøjelsgaard & Olesen, 2013). Furthermore, temperature and precipitation seasonality may also regulate plant phenology, which can affect interaction specialization among species (Borchert, 1998). For example, in seasonal environments the flowering phases are more seasonally defined, which may produce temporal flowering modules; in other words, temporary flowering peaks, where are much flowers available (Borchert, 1998; Carnicer et al., 2009; van Schaik et al., 1993). These modules, associated to short flowering phenophases, may reduce niche overlap among plants, in order to decrease competition for pollinators during these flowering periods. Moreover, pollinators may also have seasonal occurrence, generating modules of interactions and decreasing niche overlap (Bosch, Martín-González, Rodrigo, & Navarro, 2009; Carnicer et al., 2009; Martín-González, Allesina, Rodrigo, & Bosch, 2012). Nevertheless, the relationship between niche overlap and climate changes according to the pollination system. For instance, hummingbirds have a higher interaction specialization in regions with higher mean annual precipitation (Dalsgaard et al., 2011; Maruyama et al., in press.) while insects have different responses according to the group (Martín-González et al., 2009). Besides environmental factors, biological factors may also influence niche overlap. For example, networks with higher species richness decrease the chance of interspecific competition within a guild and consequently decrease niche overlap (Armbruster, 2006; Dalsgaard et al., 2011; Jordano, 1987; Martín-González et al., 2015; Olesen & Jordano, 2002). Other facets of diversity may also affect niche overlap, including functional and phylogenetic diversity. It is known that trait matching allows for a more efficient resource exploitation (Fenster,

Armbruster, Wilson, Dudash, & Thomson, 2004), which may increase the partitioning of resources among species (Maruyama, Vizentin-Bugoni, Oliveira, Oliveira, & Dalsgaard, 2014) reducing their niche overlap. Because of this, a negative relationship between functional diversity and niche overlap is expected (Dehling, Jordano, Schaefer, Böhning-Gaese, & Schleuning, 2016; Maruyama et al., in press.). Finally, phylogenetic diversity describes different evolutionary histories, which may result in different interaction patterns among clades (Rezende, Lavabre, Guimarães, Jordano, & Bascompte, 2007). Both mutualistic and antagonistic networks seem to have a phylogenetic signal in network properties such as specialization and modularity, indicating a tendency of related species to interact with the same partners (Rezende et al., 2007; Braga, Araújo, & Boeger, 2014; Martín-González et al., 2015; Rohr & Bascompte, 2014; Schleuning et al., 2014). Thus, a lower niche overlap is expected in communities with higher phylogenetic diversity.

In Neotropics, bats of Phyllostomidae family pollinate around 360 plant species (Fleming, Geiselman, & Kress, 2009). Although the underlying drivers generating niche overlap at large scales have been well studied in insect-plant interactions (Olesen & Jordano, 2002; Vázquez, Chacoff, & Cagnolo, 2009; Trøjelsgaard & Olesen, 2013) and in bird-plant pollination networks (Dalsgaard et al., 2011; Martín-González et al., 2015; Maruyama et al., in press; Zanata et al., 2017) it remains unexplored for bat-plant pollination networks. Focusing in Neotropical vertebrate pollination, birds and bats are the major vertebrate pollinators (Bawa, 1990). However, hummingbirds and bats have different evolutionary histories and interaction patterns, which is reflected in plants' and pollinators' morphologies, and pollinators' behavior (Muchhala, 2003; Fleming & Mucchala, 2008). Moreover, differences between interaction patterns of birds and bats were reported for seed-dispersal interactions (Mello et al., 2011). Therefore, the vertebrate Neotropical pollination systems

should have different patterns and drivers of niche overlap. In this sense, our aim is to identify the drivers of niche overlap in Neotropical bat-plant pollination networks. We expect a higher niche overlap in communities with lower (1) temperature seasonality, (2) precipitation seasonality, (2) guild richness, (3) functional diversity, and (4) phylogenetic diversity.

METHODS

Bat-plant pollination networks

We used a dataset of 22 published and unpublished bat-plant pollination networks (See Appendix S1 in Supporting Information, Table S1.1.), distributed from 31º43'N to 25º21'S across nine Neotropical countries (See Fig. S1.1.). Each network describes plants species used as nectar resources by bats species in a given locality, representing a community. Interactions between bats and plants were summarized in an adjacency matrix, with plants in the columns and bats in the rows. Among the twenty-two networks, twelve networks were weighted, i.e. interaction frequency among species was included. Interaction frequency is defined as the pairwise interactions among bats and plants described by the number of individuals of each bat species visiting each plant species, or as the percentage of pollen type carried by a bat species. In total, our dataset comprises 213 plant species and 45 bat species. We followed the taxonomic classification of Magallón et al. (2015) for plants and Wilson & Reeder (2005) for bats.

Niche overlap

We used the weighted mean of species complementary specialization (<*d'*>), derived from the complex network approach (Blüthgen et al., 2006) to quantify the niche overlap of each guild in weighted networks (hereafter: weighted niche overlap). This index describes interaction specialization based on the interaction frequency of each species in comparison to a null model that predicts pairwise interactions based on resource availability, represented by the marginal totals on the adjacency matrix. When a species has a pairwise interaction frequency deviated than the frequency predicted by the null model, it is considered a specialist species performing exclusive interactions. For this reason, complementary specialization may be used as an indicator of niche overlap between species (Blüthgen, 2010; Blüthgen et al., 2006). The <*d'*> can vary from zero to one, where values closer to zero represent a higher niche overlap and values closer to one represent a lower niche overlap (Blüthgen et al., 2006). We used the guild mean for each network. This metric was calculated with the "specieslevel" function in the *bipartite* package (Dormann et al., 2017) in R 3.3.3 (R Core Team, 2017).

To measure niche overlap for binary networks (hereafter: binary niche overlap), we used the Morisita-Horn index of niche overlap, $\hat{C}_H$ (Horn, 1966). This index describes the mean similarity in interaction patterns between species of the same guild, where values closer to zero indicate lower niche overlap and values closer to one indicate higher niche overlap (Dormann et al., 2017). Since $\hat{C}_H$ measures niche overlap and <*d'*> measures the exclusiveness of interactions, these indexes are opposite to each other numerically. To calculate the $\hat{C}_H$ index, we used the function "grouplevel" in the *bipartite* package in R (Dormann et al., 2017).

Drivers of niche overlap

Climate seasonality was described by the standard deviation of annual temperature and the coefficient of variation of annual precipitation of each network locality. Both variables were obtained from the *WorldClim* 2.0 database (Fick & Hijmans, 2017). Guild richness was described by the richness of plant and bat species of each network.

Functional diversity was described by the mean pairwise distance (MPD) index (Laliberté & Legendre, 2010). We selected the following traits for plants: habit and corolla's color, shape and length. As for bats, we selected forearm length, greatest length of the skull, breadth of the braincase, and length of maxillary tooth row. Both plants and bat traits were selected because they reflect adaptations to bat pollination and to optimize exploitation of nectar, respectively (Fleming et al., 2009). Traits values were obtained from the literature (see Appendix S2). To calculate the MPD of each network, we constructed a Gower's distance matrix of plants' and bats' functional traits separately. MPD describes the mean functional distance between each pair of species in the community (Webb, 2000). In this sense, higher values of MPD indicate a community with functionally distinct species (Laliberté & Legendre, 2010). The analysis was performed using the "ses.mpd" function in the *picante* package in R (Kembel et al., 2010).

Phylogenetic diversity was also described by the MPD index (Webb, 2000). This index describes the mean nodal distance between each pair of species in the community (Webb, 2000). Therefore, higher values of MPD indicate a phylogenetic diverse community. To calculate this index, we used the phylogenetic tree of Magallón et al. (2015) for plants and Shi & Rabosky (2015) for bats (See Appendix S3). Plants phylogeny was built with Phylocom 4.2 software (Webb, Ackerly, & Kembel, 2008) using the Magallón et al. (2015) as the backbone tree. MPD values were obtained using the "ses.mpd" function in the *picante*

package in the R (Kembel et al., 2010). Five bat species from our communities were missing in the Shi & Rabosky (2015) phylogeny (*Leptonycteris nivalis, Lonchophylla inexpectata, L. dekeyseri, L. hesperia* e *Xeronycteris vieirae*). Because of this, we used this phylogeny as a backbone tree and we built a new phylogeny adding the missing species as basal polytomies (but results changed when we add the missing species as terminal polytomies, see Appendix S4 for further information).

Analysis

We made multiple linear regression models using the $<d'>$ and $\hat{C}_H$ indexes as response variables for the two guilds (plants and bats). Temperature and precipitation seasonality, guild richness, functional and phylogenetic diversity were used as predictors variables. More so, we include the effect of network asymmetry (calculated according to Blüthgen et al., 2007) and sampling size (months) in the models. Analyses were performed with the "lm" function in the *stats* package (R Core Team 2017). Since climate may drive species richness and morphological traits could have phylogenetic signal (*i.e.* phylogenetic related species resembling more among each other than with non-related species, Münkemüller et al., 2012), we tested if there was a correlation between those variables using a Pearson correlation. We did not find any significant correlation between species richness and climate variables, nor between functional and phylogenetic diversity ($r < 0.36$, $P \geq 0.05$). Thus, all variables were included in the analyses. Furthermore, we did not find multicollinearity between the predictor variables, since variance inflation factor values were ≤ 2.00 (Hair, Black, Babin, & Anderson, 2010). Model selection was made with the corrected Akaike Information Criterion (AIC_c), choosing the minimum adequate model (MAM), which is the model with the lowest ΔAIC_c (Burnham & Anderson, 2002). Model selection was

performed with the "dredge" function of *MuMIn* package in R (Barton, 2016). Finally, we tested the spatial autocorrelation in the residuals of the MAM, using Moran's *I*. We performed this analysis with "correlog" function of *pgirmess* package in R (Giraudoux, 2017). Since we found spatial autocorrelation in the $\hat{C}_H$ plant model, we performed a GLS model including a ratio spatial structure. This model was made with the "gls" function of the *nlme* package in R (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2017).

RESULTS

Plant richness varied between 28 and four plants per network, whereas bat richness varied between 12 and two bats per network. Network asymmetry and sample size had not relationship with niche overlap. Weighted niche overlap was high both in plants ($<d'>$ = 0.15 ± 0.12, μ ± σ) and bats ($<d'>$ = 0.26 ± 0.27). Plants visited by nectar-feeding bats showed a higher weighted niche overlap in communities with lower precipitation seasonality and higher plant richness (R^2_{adj} = 0.53, Table 1, Fig. 1A, B-2). However, the variation of weighted niche overlap between nectar-feeding bats was not explained by any of the factors (Table 1).

Binary niche overlap was moderate for plants ($\hat{C}_H$ = 0.623 ± 0.176) and bats ($\hat{C}_H$ = 0.575 ± 0.240). Nectar-feeding bats showed a higher binary niche overlap in communities with lower bat phylogenetic diversity (R^2_{adj} = 0.13, Table 1, Fig. 1C-3). However, the variation of binary niche overlap between plants was not explained by any of the factors (Table 1).

DISCUSSION

We found that niche overlap in Neotropical bat-plant pollination networks was affected by precipitation seasonality, plant richness, and bat phylogenetic diversity. Our results show that plants have a lower weighted niche overlap in communities located in higher seasonality of precipitation areas and with lower plant richness, whereas binary bat niche overlap decreases in communities with higher bat phylogenetic diversity. These results are in accordance with our hypotheses with the exception of plant richness, given that we expected a lower niche overlap in communities with higher plant richness. On the other hand, we did not find any relationship between weighted and binary niche overlap and temperature seasonality, bat richness, bat and plant functional diversity and plant phylogenetic diversity, which is contrary to our predictions.

The negative relationship between climate seasonality and niche overlap is expected since resource availability in pollination and seed-dispersal systems is affected by climate seasonality (Carnicer et al., 2009). Plants in areas with high precipitation seasonality often adapt their phenologies to deal with water scarcity, presenting short peaks of flowering before the rainy season (Borchert, 1998; van Schaik et al., 1993). In response, pollinators are driven to adapt their foraging behavior to such conditions, favoring the formation of modules of species with overlapping phenological schedules (Carnicer et al., 2009). As a result, a reduced niche overlap among plants, associated with short flowering phenophases, may avoid competition for pollinators in these flowering periods (Armbruster, 2006; Ollerton, 2006), thus turning the short-flowered species more specialized in their interactions (Bosch et al., 2009; Martín-González et al., 2009). A similar relationship was found for bird seed-dispersal networks, where a lower niche overlap was associated with environments with high temperature seasonality (Schleuning et al., 2014; but see Sebastián-González et al., 2015).

Additionally, a local study of a bat seed-dispersal network in a seasonal region found that interactions change with rainfall seasonality, with higher number of interactions in the rainy season (Laurindo, Gregorin, & Tavares, 2017). A similar pattern was found in pollination networks in highly seasonal environments, were insects and hummingbirds have more specialized interactions in dry season (Souza et al., 2018). Thus, seasonality is likely to drives plant and pollinators phenologies resulting in short-lived modules of interacting species and hence, lower niche overlap in networks occurring in areas more seasonal.

Lower niche overlap is associated with lower plant richness. This result is different from expected, opposing the patterns found in insect and hummingbird pollination networks (Jordano, 1987; Dalsgaard et al., 2011; Martín-González et al., 2015; Olesen & Jordano, 2002). Thus, the relationship between niche overlap and plant richness remains unclear. Some authors argue that higher resource richness may represent a key driver for generalization of interactions, leading to the development of pollinators' traits that allow them to explore all resource types, therefore increasing niche overlap in communities with higher plant richness (Schleuning et al., 2012; Waser, Chittka, Price, Williams, & Ollerton, 1996). Nevertheless, if communities are not limited by resources (*i.e.* interactions), generalized interactions could be expected. When interaction specialization is associated with higher efficiency in resource use or reduced competition, a higher plant specialization is favored. However, when resources are similar and accessible, optimal foraging theory predicts interaction generalization due to a reduction in time of foraging, optimizing resource use (Albrecht, Riesen, & Schmid, 2010; Blüthgen et al., 2007; Waser et al., 1996). It is possible that resources offered by the plants in our networks are very similar to each other, leading to niche overlap in the communities. Moreover, the networks with higher plant species richness are poor in bat species (between two and four species, see Appendix 1, Table

S1.1.) favoring the niche overlap between plants. On the other hand, arid environments included in our study are poor in plant and bat richness, but each bat has a strong adaptation to nectarivory, because they belong to obligatory nectar-feeding bat subfamilies. As a result, we observed species-poor communities in arid environments with specialized interactions.

As expected, we found that bat niche overlap is negatively related to bat phylogenetic diversity. Since phylogenetically diverse communities have species with different evolutionary histories, bats from different clades are probably adapted to interact with different plant species (Rezende et al., 2007). Consequently, when non-related species coexist in a community, they tend to use different resources, decreasing niche overlap. This is especially true considering that nectarivory evolved at least twice in the evolutionary history of Phyllostomidae bats, originating two subfamilies of obligate nectar-feeding bats: Glossophaginae and Lonchophyllinae (Datzmann, von Helversen, & Mayer, 2010; Rojas, Vale, Ferrero, & Navarro, 2011). More so, communities are also composed of facultative nectar-feeding bats, which belong to other subfamilies, that can access different resources compared to obligatory nectar-feeding bats (Bolzan, Pessôa, Peracchi, & Strauss, 2015; Datzmann et al., 2010; Rojas et al., 2011). Consequently, the presence of obligatory and facultative nectar-feeding bats increases phylogenetic diversity, promoting lower bats niche overlap. However, though cranial morphologies of phyllostomid nectar-feeding bats are different, since the degree of elongation of the rostrum is associated with the phylogenetic history of each lineage (Bolzan et al., 2015), those differences are not reflected in bats functional diversity. This could occur because we did not include traits as foraging behavior or tongue morphology and because a cranial morphological convergence could occur, since morphometric space of obligatory nectar-feeding bats is overlapped (Bolzan et al., 2015; Monteiro & Nogueira, 2011). Thus, traits sectioned for our study may not allow us to

distinguish between subfamilies on bats phylogeny, founding a similar functional diversity between them. The relation between niche overlap and phylogenetic relatedness has been largely discussed in community ecology. For example, evolutionary distant plant species tend to have a lower degree of competition, resulting in a lower niche overlap (Godoy, Kraft, & Levine, 2014). Furthermore, in mutualistic networks, phylogenetically related species have a similar number of interactions per species and similar roles, especially among pollinators (Rezende et al., 2007). Moreover, different authors have found an effect of evolutionary history in species interaction, indicating a relationship between phylogenetic signal and network properties. For instance, complementary specialization and modularity are associated to the phylogenetic signal in hummingbird interaction with plants, suggesting that resource partitioning and interspecific competition among related hummingbirds could be structuring the plant-hummingbird interactions (Martín-González et al., 2015). Furthermore, phylogenetic signal was also detected in degree, modularity and, within-module connectivity in avian seed-dispersal networks (Schleuning et al., 2014). Phylogenetic signal of interactions has been also reported in antagonistic networks as stronger than in mutualistic networks (Rohr & Bascompte, 2014). Specifically in parasitic networks, more closely-related hosts tend to be clustered in modules (Braga et al., 2014; Ives & Godfray, 2006; Krasnov et al., 2012).

Our results report a higher niche overlap in bat-plant pollination networks, compared to other pollination systems (Blüthgen et al., 2007; Dalsgaard et al., 2011; Olesen, Dupont, Ehlers, & Hansen, 2007; Watts, Dormann, Martín-González, & Ollerton, 2016; Zanata et al., 2017). This contrasting niche overlap may arise because flowers visited by bats tend to have less restrictive morphologies than flowers visited by other animals (Fleming, Muchhala, & Ornelas, 2005). In this regard, chiropterophily adaptations result in flower morphologies that

are easier to access by all bat species in the community (Gonzalez-Terrazas, Medellin, Knornschild, & Tschapka, 2012). This can be seen in bell- or dish-shaped flowers, which could receive visits from more bat species than other floral shapes (Fleming et al., 2009; Olesen, Bascompte, Dupont, & Jordano, 2007). More so, since nectar-feeding bats can change their diet to fruit and insects when nectar is scarce, they would be less specialized on their nectar resources compared to hummingbirds, which generally do not switch their diets (Fleming et al., 2005). On the other hand, evolutionary differences between hummingbirds and bats might play an important role on interaction specialization of both groups. Hummingbirds and nectar-feeding bats evolved in similar times (hummingbirds 22 Mya ago and bats 29-20 Mya ago) and there were a radiation in the both groups (Datzmann et al., 2010; McGuire et al., 2014; Monteiro & Nogueira, 2011). Despite this, radiation of hummingbirds was associated with pollination interaction with plants, while the adaptive radiation of bats was associated with different kind of diets (carnivory, frugivory, sanguivory and nectarivory; Fleming et al., 2005; Monteiro & Nogueira, 2011). Consequently, there are more plants associated with hummingbirds than with nectar-feeding bats and current communities tend to have more specialized hummingbird flowers than bat flowers (Fleming et al., 2005). Curiously, bat seed-dispersal networks are also more generalist than bird seed-dispersal networks, which has been related to the different patterns of frugivory evolution in avian and bat clades (Mello et al., 2011). Differences in bird and bat niche overlap in both pollination and seed-dispersal mutualistic networks indicate that differential evolutionary histories in birds and bats are consistently reflected on their interaction patterns.

Although our study increases the knowledge about the patterns of niche overlap in vertebrate pollination systems, the generality of our results might be limited by the lower number of studies and lower plants taxonomic resolution in bat-plant pollination systems,

when compared to other pollination systems. Furthermore, the interactions and interaction frequencies between bats and plants are harder to register than plant interactions with insects and birds, as well as their interaction frequencies, which may be subsampled in bat-plant pollination networks. These methodological challenges may overestimate interaction specialization (Blüthgen, 2010; Bosch et al., 2009). However, our networks showed a high niche overlap, suggesting that the high generalization within the guild is not biased by frequency of interaction sampling.

In conclusion, we found that weighted plant niche overlap in Neotropical bat-plant pollination networks is higher in communities with lower precipitation seasonality and higher plant richness, while binary bat niche overlap is a higher in communities with lower bat phylogenetic diversity. Furthermore, the niche overlap in Neotropical bat-plant pollination networks is higher when compared with other Neotropical pollination systems. Our results reinforce the importance of climate seasonality and species richness on the niche overlap of mutualistic interactions, and highlight the importance of considering species evolutionary history while investigating the drivers of community niche overlap.

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ADDITIONAL SUPPORTING INFORMATION:

Appendix S1. Location, details and sources of the bat-plant networks

Appendix S2. List of functional traits references for bat and plants

Appendix S3. Bat and plant phylogenies

Appendix S4. Methods and results when using a bat phylogeny with polytomies located in terminal nodes

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Tables

Table 1 – Drivers of weighted (complementary specialization, $<d'>$) and binary (Morisita-Horn Index, $\hat{C}_H$) niche overlap of Neotropical bat-plant pollination networks predicted by multiple linear regression models. A dash indicates that the predictor variable was absent in the minimum adequate model (MAM). Numbers in parenthesis indicate sample size used in each analysis.

	Complementary specialization $<d'>$ (12)						Morisita-Horn Index $\hat{C}_H$ (22)								
	Plants			Bats			Plants						Bats		
	Σw_i	AVM	MAM	Σw_i	AVM	MAM	Σw_i	AVM	MAM	Σw_i[§]	AVM[§]	MAM[§]	Σw_i	AVM	MAM
TS	0.05	0.02	-	0.09	-0.00	-	0.14	-0.00	-	0.00	0.01	-	0.34	-0.06	-
PS	0.74	0.10	0.10	0.12	0.04	-	0.70	-0.05	-0.04	0.06	-0.04	-	0.20	-0.04	-
GR	0.56	-0.10	-0.10	0.27	-0.08	-	0.22	-0.02	-	0.00	-0.03	-	0.19	-0.04	-
FD	0.07	-0.04	-	0.08	-0.00	-	0.15	-0.00	-	0.01	-0.00	-	0.23	-0.04	-
PD	0.32	-0.09	-	0.18	0.06	-	0.17	-0.01	-	0.00	-0.00	-	0.50	-0.08	-0.09
NA	0.08	0.04		0.11	0.03	-	0.36	-0.04	-	0.00	-0.05	-	0.14	-0.00	-
SE	0.05	-0.00		0.18	-0.06	-	0.22	-0.00	-	0.00	-0.00	-	0.23	-0.05	-
R^2_{adj}			0.53			-			0.15			-			0.13
Moran's *I*			$\leq 0.25^{NS}$			-			$\leq 0.38^{*}$			-			$\leq 0.13^{NS}$

FD: Functional diversity, GR: Guild richness, NA: Network asymmetry, PD: Phylogenetic diversity, PS: Precipitation seasonality, SE: Sampling effort, TS: Temperature seasonality. Σw_i: mean importance of each predictor variable measured across all models which accumulated sum higher than 0.95; AVM: standardized coefficients of the averaged model; MAM, standardized coefficients of the minimum adequate model with the lowest ΔAIC_c. R^2_{adj}: variation explained by the minimum adequate model with the lowest ΔAIC_c. NS: $p>0.05$, $*p\leq 0.05$. [§]Results for plants' GLS model without spatial autocorrelation.

Figures

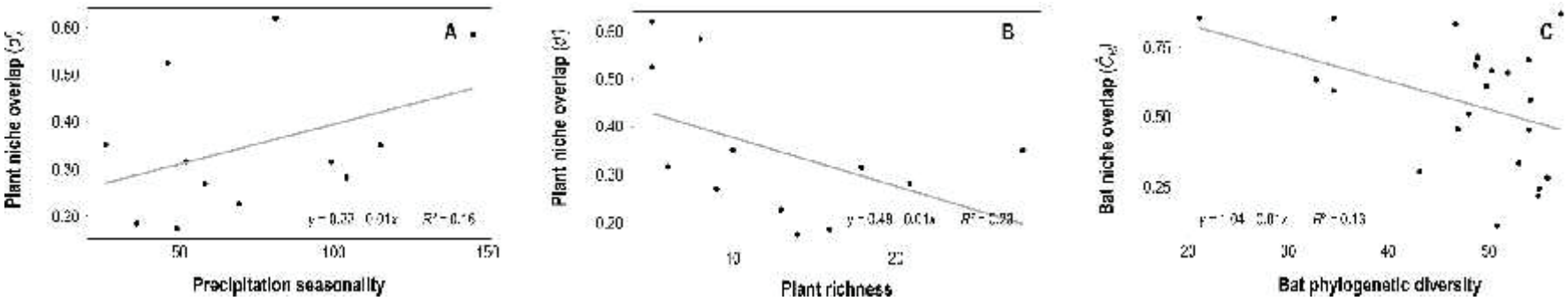

Figure 1 – Relationship between plant niche overlap and precipitation seasonality (A) and plant richness (B) and relationship between bat niche overlap and bat phylogenetic diversity (C) in Neotropical bat-plant pollination networks.

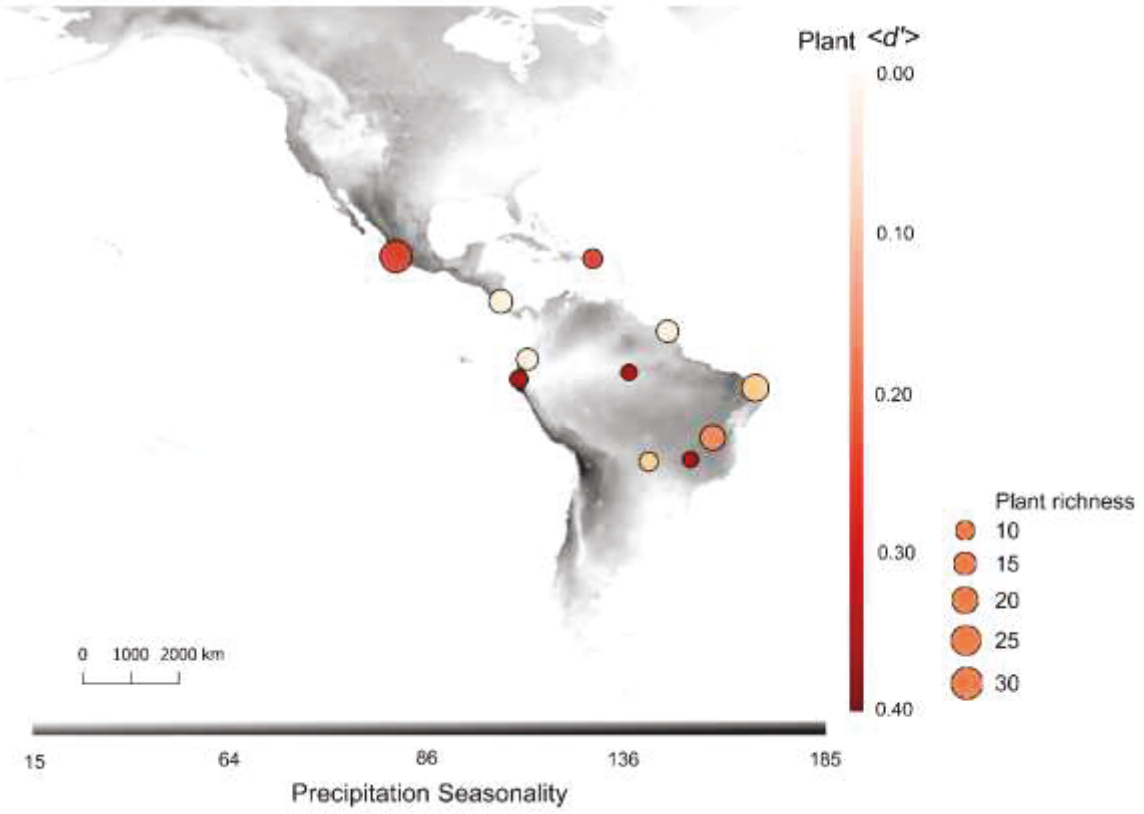

Figure 2 – Drivers of plant niche overlap (<*d'*>) in twelve weighted bat-plant pollination networks in Neotropics. Lower niche overlap is represented by red shades, with higher niche overlap in paler shades. The precipitation seasonality is represented in grey shade, while the plant richness is represented by circle sizes. Two pollination networks from Costa Rica are overlapped in the figure.

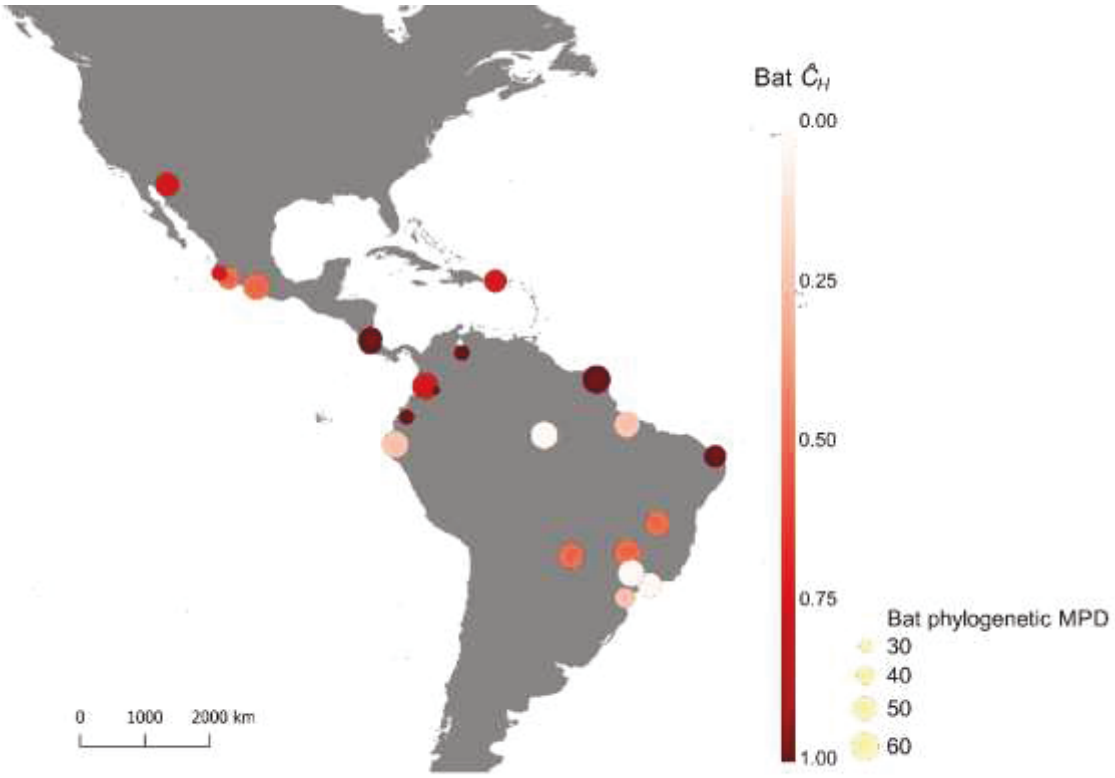

Figure 3 – Driver of bat niche overlap ($\hat{C}_H$) in twenty-two binary bat-plant pollination networks in the Neotropics. Lower niche overlap is represented by red shades, with higher niche overlap in darker shades. Bat phylogenetic diversity is represented by circle sizes. Two pollination networks from Costa Rica are overlapped in the figure.

Supporting Information

Appendix S1 - References and location of the networks used in the analysis.

Table S1.1. - Information about the 22 networks used in the analysis. Type refers if network is weighted (W) or binary (B). Sampling size in months. fMPD: Functional mean pairwise distance (MPD). pMPD: Phylogenetic mean pairwise distance (MPD). $<d'>$: weighted niche overlap (complementary specialization). $\hat{C}_H$: binary niche overlap (Morisita-Horn Index).

Reference	Latitude	Longitude	Type	Plant richness	Bat richness	Plant fMPD	Plant pMPD	Bat fMPD	Bat pMPD	Network assymetry	Sampling size	Plant $<d'>$	Bat $<d'>$	Plant $\hat{C}_H$	Bat $\hat{C}_H$
Arias *et al.*, 2009	-4.1406	-80.5869	W	8	3	0.732	233.708	0.131	55.033	-0.454	24	0.341	0.524	0.358	0.214
Carvalho, 1961	-1.4525	48.4764	B	7	3	0.679	192.650	0.504	53.138	-0.400	-	-	-	0.524	0.333
Cordero, 2016	-5.7981	-36.2411	W	21	4	0.686	230.808	0.072	46.800	-0.680	6	0.079	0.180	0.480	0.834
Fischer, 2000	-2.8833	-59.9333	W	5	3	0.675	180.070	0.287	55.975	-0.250	12	0.276	0.614	0.392	0.279
Geiselman, 2010	4.8333	-52.7000	W	14	2	0.802	217.288	0.270	57.353	-0.750	24	0.030	0.120	0.700	0.870
Gonçalves, 2010	-19.5747	-56.2436	W	9	12	0.692	209.839	0.334	51.984	0.143	33	0.072	0.096	0.653	0.659
Heithaus *et al.*, 1975	9.9000	-84.0500	W	6	7	0.489	207.718	0.285	49.010	0.08	24	0.099	0.088	0.733	0.715
Hevly, 1979	31.7179	-112.2012	B	8	2	0.762	248.869	0.119	50.394	-0.600	-	-	-	0.810	0.667
Mora, 2017	3.8775	76.4380	B	6	6	0.783	205.812	0.236	54.091	0	2	-	-	0.613	0.706

Reference	Latitude	Longitude	Type	Plant richness	Bat richness	Plant fMPD	Plant pMPD	Bat fMPD	Bat pMPD	Network assymetry	Sampling size	Plant <d'>	Bat <d'>	Plant $\hat{C}_H$	Bat $\hat{C}_H$
Muchhala & Jarrín-V, 2002	-0.4167	-79.0000	W	13	2	0.752	223.470	0.134	32.821	-0.733	9	0.051	0.204	0.716	0.634
Pedro 1992	-19.1556	-48.3889	W	5	5	0.611	202.833	0.113	54.307	0	36	0.384	0.292	0.513	0.561
Pinto 2010	-15.0833	-44.2167	W	18	6	0.708	226.061	0.122	49.894	-0.500	12	0.099	0.228	0.447	0.611
Ruiz *et al.,* 1997	3.2833	-74.9667	B	4	2	0.667	145.142	0.052	21.143	-0.333	12	-	-	0.833	0.857
Salmerón *et al.,* 2008	17.5983	-99.8275	B	10	4	0.822	238.326	0.143	54.098	-0.428	12	-	-	0.733	0.453
Sazima *et al.,* 1999	-23.5833	-45.3333	B	14	5	0.849	235.992	0.121	50.945	-0.473	36	-	-	0.527	0.107
Silva 2009	-25.3500	-48.7667	B	13	8	0.798	232.897	0.341	43.237	-0.238	36	-	-	0.478	0.301
Sosa & Soriano, 1993	8.4878	-71.3361	B	4	2	0.625	157.166	0.200	34.545	-0.333	12	-	-	0.833	0.857
Soto-Centeno & Kurta, 2006	18.4167	-66.7167	W	10	2	0.670	222.267	0.249	48.094	-0.667	4	0.123	0.426	0.782	0.509
Sperr *et al.,* 2011	18.8167	-103.6333	W	28	4	0.765	226.769	0.235	46.995	-0.750	3	0.123	0.320	0.421	0.456
Stoner, 2002	19.4877	-104.9954	B	26	2	0.810	227.142	0.252	34.545	-0.857	12	-	-	0.751	0.595
Teixeira 2010	-21.9667	-47.8333	B	8	7	0.679	220.945	0.168	55.159	-0.07	24	-	-	0.452	0.240
Tschapka, 2004	10.4333	-83.9833	W	16	4	0.754	226.663	0.178	48.750	-0.600	26	0.034	0.128	0.729	0.685

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Figure S1.1. - Distribution of 22 bat-plant pollination networks across the Neotropics (31º43'N to 25º21'S).

Appendix S2 - References used to obtain the plants and bats traits data.

Table S2.1. - References of plants and bats traits. Some plants are not included on functional diversity analysis due to lacking information.

Species	Reference	Species	Reference
PLANTS			
ACANTHACEAE		FABACEAE	
Dicliptera sericea	Martius, 1874	*Eperua falcata*	Cowan, 1975; Geiselman, 2010
Thyrsacanthus sp1	Jardim Botânico do Rio do Janeiro, 2017c	*Eperua rubiginosa*	Cowan, 1975; Geiselman, 2010
AMARANTHACEAE		*Hesperalbizia occidentalis*	Rico-Arce et al., 2008; Andrade et al., 2012
Amaranthaceae sp1	Vibrans, 2009	*Hymenaea courbaril*	Leite, 2007; Geiselman, 2010; Conabio, 2013
ANACARDIACEAE		*Hymenaea* sp1	Leite, 2007; Geiselman, 2010; Conabio, 2013; Espinoza, 2013
Anacardiaceae sp1	Gentry, 1992	*Hymenaea* sp2	Leite, 2007; Geiselman, 2010; Conabio, 2013
Anacardium sp1	Martius, 1874; Freitas & Paxton, 1996	*Hymenaea stigonocarpa*	Gibbs et al., 1999; Teixeira, 2010
ARECACEAE		*Inga affinis*	Amorim et al., 2009; Silva, 2009; Sousa, 2009
Calyptrogyne ghiesbreghtiana	Cunningham, 1995; Missouri Tropical Garden, 2009a	*Inga densiflora*	Missouri Tropical Garden, 2009b
Cocos nucifera	Ulloa-Ulloa, 2009a	*Inga punctata*	Koptur, 1983; Missouri Tropical Garden, 2009c
ASPARAGACEAE		*Inga semialata*	Amorim et al., 2009; Silva, 2009
Agave americana	Gentry, 1982	*Inga edulis*	CATIE, 2000; Amorim et al., 2009; Silva, 2009
Agave ortgiesiana	Gentry, 1982	*Inga* sp1	Geiselman, 2010
Agave sp1	Rocha et al., 2005	*Inga* sp2	Silva, 2009
Agave sp2	Rocha et al., 2005	*Inga vera*	Amorim et al., 2009
Yucca sp1	Gentry, 1992	*Leucaena leucocephala*	Vibrans, 2011
BETULACEAE		*Mucuna holtonii*	Missouri Tropical Garden, 2009e

Species	Reference
Alnus sp1	Furlow, 1979; Gentry, 1992
Bignoniaceae	
Crescentia alata	Conabio, 2010c; Rodríguez-Peña et al., 2016
Crescentia cujete	Lemke, 1984, 1985; Silva, 2009; López et al., 2014
Crescentia sp1	Montiel, 1991; Conabio, 2010c; Rodríguez-Peña et al., 2016
BIXACEAE	
Bixa sp1	Liogier, 1994; Roubik, 1995
BORAGINACEAE	
Cordia gerascanthus	Opler et al., 1975
BROMELIACEAE	
Encholirium spectabile	Martius, 1874
Pitcairnia brongniartiana	Smith & Downs, 1974; Muchhala & Jarrín-V, 2002; Amorim et al., 2009
Vriesea atra	Martius, 1874; Silva, 2009
Vriesea bituminosa	Sazima et al., 1999
Vriesea gigantea	Sazima et al., 1999
Vriesea longiscapa	Sazima et al., 1999
Vriesea platynema	Silva, 2009
Vriesea sazimae	Sazima et al., 1999
Vriesea sp1	Sazima et al., 1999; Silva, 2009
CACTACEAE	
Armatocereus cartwrightianus	Ostalaza-Nano, 2006
Cephalocereus sp1	Gibson & Horak, 1978; Rowley, 1980
Mucuna urens	Sazima et al., 1999; Amorim et al., 2009; Silva, 2009
Parkia gigantocarpa	Hopkins, 1986; Fischer, 2000
Parkia nitida	Hopkins, 1986; Fischer, 2000; Geiselman, 2010
Parkia pendula	Hopkins, 1986; Fischer, 2000
Prosopis juliflora	FAO; Conabio, 2010e
Schnella guianensis	Hokche & Ramirez, 1990; Geiselman, 2010
Schnella siqueiraei	Vaz, 1979; Hokche & Ramirez, 1990; Geiselman, 2010
Zapoteca formosa	Hernandez, 1989; Missouri Tropical Garden, 2009h
LECYTHIDACEAE	
Lecythis poiteaui	Fischer, 2000; Geiselman, 2010; Matta & Scudeller, 2012
LORANTHACEAE	
Psittacanthus acinarius	Kuijt, 2009; Geiselman, 2010
Psittacanthus corynocephalus	Kuijt, 2009
LYTHRACEAE	
Lafoensia vandelliana	Martius, 1874; Sazima et al., 1999
Lafoensia glyptocarpa	Sazima et al., 1999
Lafoensia pacari	Lourteig, 1986; Sazima et al., 1999; Teixeira, 2010
MALVACEAE	
Abutilon regnellii	Buzato et al., 1994; Sazima et al., 1999; Takeuchi & Lopes-Esteves, 2012
Abutilon reflexum	Macbride, 1956; Burandt & Fryxell, 1990
Bombacoideae sp1	UDELAR, 2017
Ceiba aesculifolia	Standley, 1920; Herrerías-Diego et al., 2006; Rodríguez-Peña et al., 2016

Species	Reference
Cereus repandus	Britton & Rose, 1920
Melocactus zehntneri	Leal et al 2006 Leal et al., 2006
Pachycereus pecten-aboriginum	Britton & Rose, 1920; Molina-Freaner & Eguiarte, 2003; Rodríguez-Peña et al., 2016
Pilosocereus gounellei	Rocha & Agra, 2002
Pilosocereus pachycladus	Jardim Botânico do Rio do Janeiro, 2017a
Pilosocereus tillianus	Office of Foreign Seed and Plants Introduction, 1922; Figueredo-Urbina, 2006
Praecereus euchlorus-smithianus	Britton & Rose, 1920
Stenocereus chrysocarpus	Arreola -Navas & Terrazas, 2003; Rodríguez-Peña et al., 2016
Stenocereus griseus	Britton & Rose, 1920; Nassar et al., 1997
Stenocereus sp1	Gibson & Horak, 1978; Sperr et al., 2011
Stenocereus standleyi	Gibson & Horak, 1978; Rodríguez-Peña et al., 2016
Weberocereus tunilla	Britton & Rose, 1920; Tschapka et al., 1999; Missouri Tropical Garden, 2009g
CAMPANULACEAE	
Burmeistera sodiroana	Muchhala & Jarrín-V, 2002; Muchhala, 2006
Burmeistera succulenta	Muchhala, 2006
Burmeistera truncata	Muchhala, 2006
Siphocampylus sulfureus	Sazima et al., 1994; FloraSBS, 2005
CANNACEAE	
Cannaceae sp1	Gentry, 1992
CAPPARACEAE	
Ceiba pentandra	Standley, 1920; Gribel et al., 1999; Lobo et al., 2005
Ceiba sp1	Menino et al., 2015
Ceiba trichistandra	Herbarium New York Botanical Garden, 1970a; Aguirre-Mendoza, 2012
Cavanillesia sp1	Almeida, 2012
Chiranthodendron pentadactylon	Larreátegui, 1805; UNAM, 2009
Eriotheca pentaphylla	Sazima et al., 1999
Eriotheca squamigera	Robyns & Nilsson, 1981; Duarte & Esteves, 2011
Helicteres baruensis	Goldberg, 2009; Rodríguez-Peña et al., 2016
Hibiscus sp1	Hamilton, 1932
Luehea grandiflora	Teixeira, 2010; Araújo et al., 2013
Luehea paniculata	Macbride, 1956; Barbosa-Filho & de Araujo, 2013
Luehea sp1	Padilla-Velarde et al., 2006; Missouri Tropical Garden, 2009d
Matisia bracteolosa	Smith, 1897; Cascante-Marín, 1997
Ochroma pyramidale	Conabio, 2010d
Ochroma sp1	Conabio, 2010d
Pachira insignis	Lequel, 1825; Geiselman, 2010
Pseudobombax ellipticum	Kunth, 1821; Eguiarte et al., 1987; Rodríguez-Peña et al., 2016
Pseudobombax grandiflorum	Martius, 1874; Silva, 2009
Pseudobombax longiflorum	Teixeira, 2010
Pseudobombax sp1	Missouri Tropical Garden, 2009f; Cielo-Filho et al., 2012

Species	Reference
Crateva palmeri	Cornejo & Iltis, 2015
Crateva tapia	Miller, 1807; Herbarium New York Botanical Garden, 1970b
Cleome spinosa	Missouri_Plants, 2002
CARYOCARACEAE	
Caryocar brasiliense	FAO, 1987; Gribel & Hay, 1993; Teixeira, 2010
Caryocar glabrum	FAO, 1987; Fischer, 2000; Geiselman, 2010
Caryocar pallidum	FAO, 1987; Fischer, 2000
CLUSIACEAE	
Clusia sp1	Amorim et al., 2009
COMBRETACEAE	
Combretaceae sp1	Rendón-Sandoval, 2009
Combretum sp1	Schemske, 1980; Pagaza-Calderón & Fernández-Nava, 2005; Ulloa-Ulloa, 2009b
Combretum sp2	Rendón-Sandoval, 2009
CONVOLVULACEAE	
Ipomoea ampullacea	Wilkin, 1995; Rodríguez-Peña et al., 2016
Ipomoea sp1	Gentry, 1992
Ipomoea sp2	Gentry, 1992
Ipomoea sp3	Gentry, 1992
Operculina sp1	Austin et al., 2011; Moreira et al., 2015
Operculina sp2	Austin et al., 2011; Moreira et al., 2015
CUCURBITACEAE	
Cucumis melo	Eisikowitch, 1988; Moreno, 2004
Pseudobombax sp2	Missouri Tropical Garden, 2009f; Cielo-Filho et al., 2012
Quararibea cordata	Bonpland, 1808; Cascante-Marín, 1997; Amorim et al., 2009
Quararibea ochrocalyx	Martius, 1874; Lopes-Esteves, 2005; Amorim et al., 2009
Quararibea parvifolia	Oliveira et al., 2004; Tschapka, 2004; Missouri Tropical Garden, 2013a
Thespesia grandiflora	Little Jr. & Wadsworth, 1964; Rivera-Ocasio, 2012
MARCGRAVIACEAE	
Marcgravia coriacea	Martius, 1874; Sazima et al., 1999; Geiselman, 2010
Marcgravia polyantha	Sazima et al., 1999; Silva, 2009
Marcgravia sp1	Sazima et al., 1999
Souroubea guianensis	Machado & Lopes, 2000; Geiselman, 2010; Jardim Botânico do Rio do Janeiro, 2017b
MELASTOMATACEAE	
Meriania pichinchensis	Wurdack, 1982; Muchhala & Jarrín-V, 2002
MORACEAE	
Brosimum alicastrum	Trécul, 1847; Conabio, 2010b
Brosimum sp1	Trécul, 1847
MUNTINGIACEAE	
Muntingia calabura	Figueiredo et al., 2008
MUSACEAE	
Musa paradisiaca	Silva, 2009
MYRTACEAE	
Psidium guajava	Granado, 2011
Psidium sp1	Granado, 2011

Species	Reference
Cucurbita argyrosperma	Vidal et al., 2006; Vibrans, 2010
Cucurbitaceae sp1	Gentry, 1992
EUPHORBIACEAE	
Aparisthmium sp1	Cielo-Filho et al., 2012; Missouri Tropical Garden, 2016
Hura polyandra	Felger et al., 2001; Oliveira et al., 2013
FABACEAE	
Albizia lebbeck	Conabio, 2010a
Alexa grandiflora	Ramirez, 1995
Anadenanthera sp 1	Altschul, 1964; Secco, 2004; Kiill & Silva, 2016
Bauhinia cheilantha	Martius, 1874; Gutiérrez, 2010
Bauhinia forficata	Gutiérrez, 2010; Neto, 2013
Bauhinia longifolia	Vaz & Tozzi, 2003; Teixeira, 2010
Bauhinia pauletia	Hokche & Ramirez, 1990; Rodríguez-Peña et al., 2016
Bauhinia rufa	Vaz & Tozzi, 2003; Teixeira, 2010
Bauhinia sp1	Rodríguez-Peña et al., 2016
Bauhinia sp2	Rodríguez-Peña et al., 2016
Bauhinia sp3	Rodríguez-Peña et al., 2016
Bauhinia ungulata	Opler et al., 1975; Hokche & Ramirez, 1990; Araújo et al., 2013
Calliandra sp1	Lemke, 1985
Coursetia rostrata	Martius, 1874; Queiroz & Lavin, 2011
Elizabetha paraensis	Muséum National d'histoire naturelle, 1998
Eperua duckeana	Cowan, 1975; Fischer, 2000
Syzygium jambos	Silva, 2009; Missouri Tropical Garden, 2013b
PASSIFLORACEAE	
Passiflora sp1	Gentry, 1992
Passiflora sp2	Gentry, 1992
Tetrastylis ovalis	Amorim et al., 2009
PROTEACEAE	
Roupala sp1	Aublet, 1775
ROSACEAE	
Eriobotrya japonica	Fang et al., 2012
RUBIACEAE	
Hillia illustris	Sazima et al., 1999; Silva, 2009; Geiselman, 2010
SAPOTACEAE	
Manilkara sapota	Gilman & Watson, 2010
Manilkara sp1	Glander & Nisbett, 1996; Zamora-Villalobos, 2000
SOLANACEAE	
Datura sp1	Raguso et al., 2003; Vibrans, 2009
Dyssochroma viridiflora	Sazima et al., 2003
Markea sp1	Muchhala & Jarrín-V, 2002
Merinthopodium neuranthum	Knapp et al., 1997
URTICACEAE	
Cecropia sp1	Berg et al., 2005
Cecropia sp2	Berg et al., 2005
BATS (PHYLLOSTOMIDAE)	
CAROLLIINAE	LONCHOPHYLLINAE

Species	Reference
Carollia brevicauda	Baker et al., 2002; Tirira, 2007
Carollia perspicillata	Cloutier & Thomas, 1992
	GLOSSOPHAGINAE
Anoura caudifer	Oprea et al., 2009
Anoura fistulata	Muchhala et al., 2005
Anoura geoffroyi	Ortega & Alarcón-D, 2008
Choeroniscus godmani	Sanborn, 1954; Solmsen, 1998
Choeronycteris mexicana	Arroyo-Cabrales et al., 1987
Erophylla sezekorni	Buden, 1976; Baker et al., 1978; Timm & Genoways, 2003
Glossophaga commissarisi	Webster & Jones, 1993
Glossophaga longirostris	Webster et al., 1998
Glossophaga soricina	Alvarez et al., 1991
Hylonycteris underwoodi	Jones Jr. & Homan, 1974
Leptonycteris curasoae	Swanepoel & Genoways, 1979; Cole & Wilson, 2006
Leptonycteris nivalis	Swanepoel & Genoways, 1979; Hensley & Wilkins, 1988
Leptonycteris yerbabuenae	Swanepoel & Genoways, 1979; Cole & Wilson, 2006
Lichonycteris obscura	Swanepoel & Genoways, 1979
Monophyllus redmani	Homan & Jones Jr., 1975
Musonycteris harrisoni	Swanepoel & Genoways, 1979; Tellez & Ortega, 1999
Lonchophylla mordax	Moratelli & Dias, 2015
Loncophylla robusta	Swanepoel & Genoways, 1979
Lonchophylla thomasi	Swanepoel & Genoways, 1979
Xeronycteris vieirae	Gregorin & Ditchfield, 2005
	PHYLLOSTOMINAE
Chrotopterus auritus	Medellin, 1989
Lophostoma brasiliense	Smith, 2008; Velazco & Gardner, 2012
Lophostoma silvicolum	Swanepoel & Genoways, 1979; Medellín & Arita, 1989
Phyllostomus discolor	Swanepoel & Genoways, 1979; Kwiecinski, 2006
Phyllostomus hastatus	Santos et al., 2003; Velazco & Gardner, 2012
	STENODERMATINAE
Artibeus fimbriatus	Dias & Peracchi, 2008; Barquez et al., 2011
Artibeus jamaicensis	Ortega & Castro-Arellano, 2001
Artibeus lituratus	Tirira, 2007; Marchán-Rivadeneira et al., 2012
Artibeus obscurus	Dias & Peracchi, 2008
Artibeus phaeotis	Swanepoel & Genoways, 1979; Timm, 1985
Artibeus planirostris	Hollis, 2005
Dermanura azteca	Swanepoel & Genoways, 1979; Webster & Jones, 1982
Platyrrhinus lineatus	Swanepoel & Genoways, 1979

Species	Reference	Species	Reference
	LONCHOPHYLLINAE	*Platyrrhinus recifinus*	Swanepoel & Genoways, 1979
Lionycteris spurrelli	Swanepoel & Genoways, 1979	*Pygoderma bilabiatum*	Swanepoel & Genoways, 1979; Webster & Owen, 1984
Lonchophylla dekeyseri	Moratelli & Dias, 2015	*Sturnira lilium*	Gannon et al., 1989
Lonchophylla hesperia	Swanepoel & Genoways, 1979	*Sturnira ludovici*	Swanepoel & Genoways, 1979
Lonchophylla inexpectata	Moratelli & Dias, 2015	*Sturnira oporaphilum*	Velazco & Patterson, 2014

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Appendix S3 – Plant and bat phylogenies

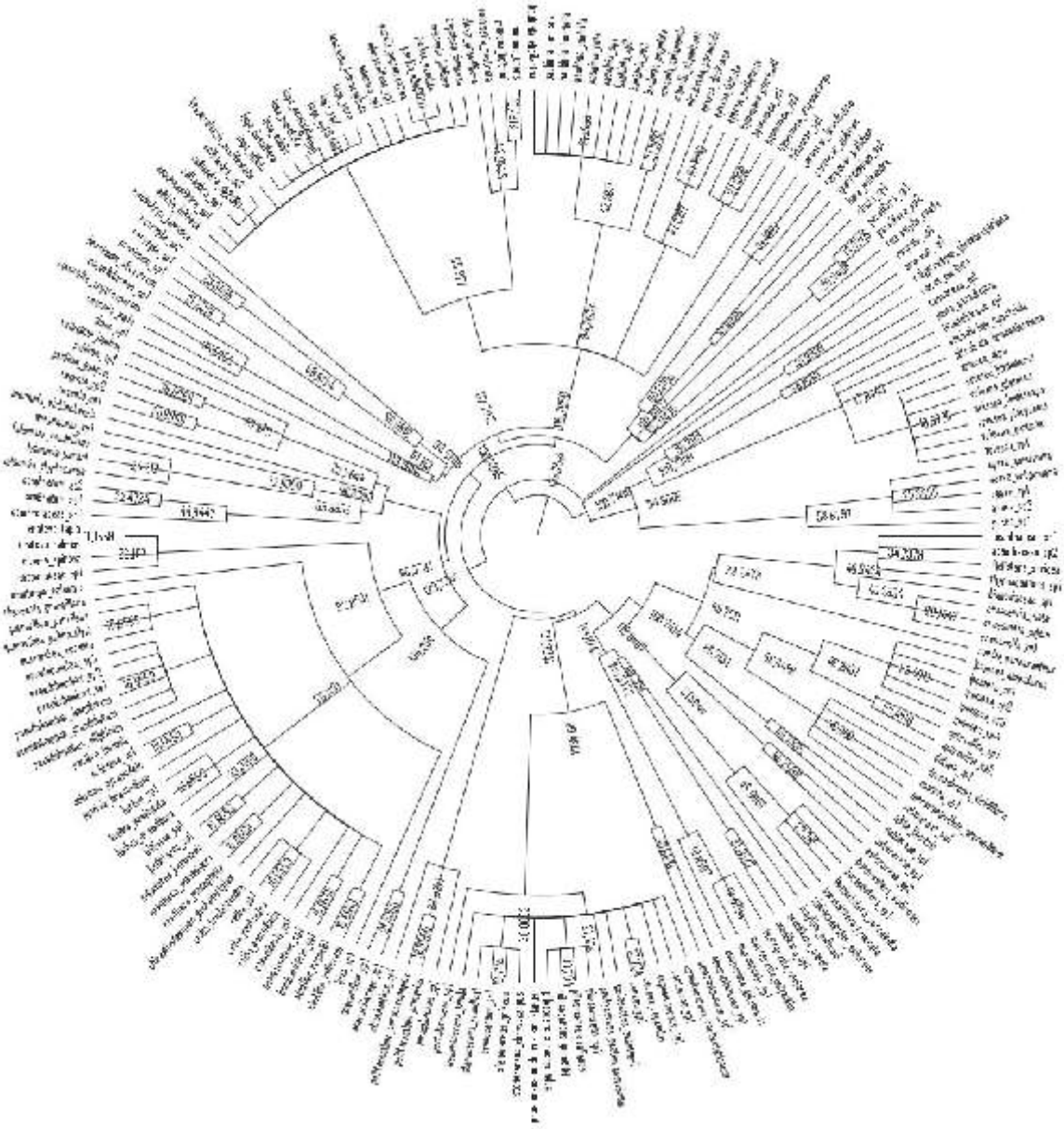

Figure S3.1A - Plant phylogeny (Based on Magallón et al. 2015, see methods for further information)

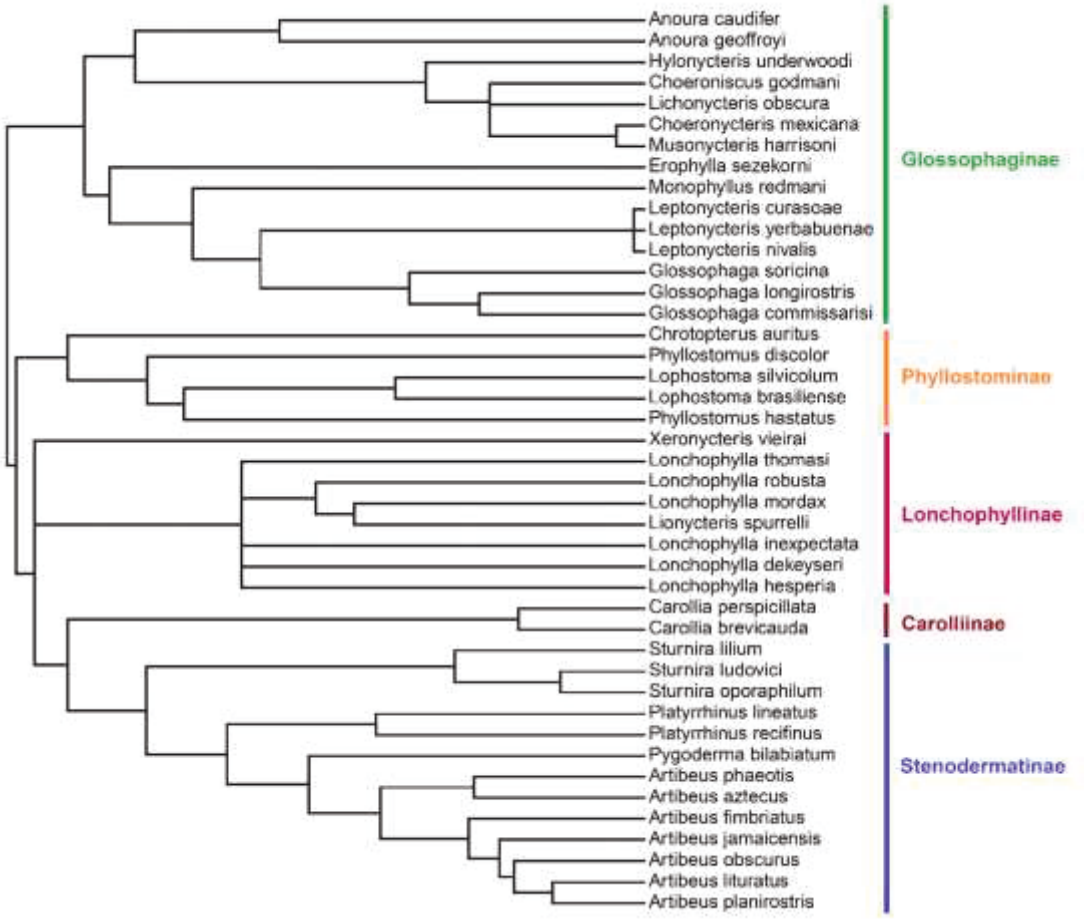

Figure S3.1B - Bat phylogeny with basal polytomies (Based on Shi & Rabosky 2015, see methods for further information). Obligatory nectar-feeding bats are included in the subfamilies Glossophaginae and Lonchophyllinae.

Appendix S4 - Results with bat phylogeny construed with terminal polytomies

We used the bat phylogeny proposed by Shi & Rabosky (2015) to obtain the phylogenetic MPD for bats. However, five bat species from our communities were missing in this phylogeny. Because of this, we use Shi & Rabosky (2015) phylogeny as a backbone tree and we built a new phylogeny adding the missing species as basal and terminal polytomies. See the main text for more details of methods. In the main text, we present results of bat niche overlap with phylogenetic MPD obtained from basal polytomies. Here, we present the results of niche overlap for weighted and binary bats networks when using a phylogenetic MPD calculated from terminal polytomies. For weighted niche overlap, we obtained the same results using both, phylogenetic diversity obtained from phylogenies with basal and terminal polytomies. Nevertheless, results changed for binary niche overlap, finding that variation of niche overlap were not explained by any the determinants (Table S4.1).

Table S4.1. - Bat niche overlap of Neotropical bat-plant pollination networks, weighted niche overlap (<*d'*>) and binary niche overlap ($\hat{C}_H$), predicted by multiple linear regression models when using phylogenetic MPD obtained from a phylogeny with terminal polytomies. A dash indicates that the predictor variable was absent in the minimum adequate model (MAM). Numbers in parenthesis are sample size used in each analysis.

	Complementary specialization <*d'*> (12)			Morisita-Horn Index $\hat{C}_H$ (22)		
	Σw_i	AVM	MAM	Σw_i	AVM	MAM
TS	0.09	-0.00	-	0.37	-0.07	-
PS	0.13	0.04	-	0.23	-0.04	-
GR	0.28	-0.08	-	0.23	-0.05	-
FD	0.08	-0.00	-	0.27	-0.05	-
PD	0.08	0.01	-	0.17	-0.03	-
NA	0.11	0.03	-	0.16	-0.01	-
SE	0.16	-0.05	-	0.25	-0.05	-
R^2_{adj}			-			-
Moran's I			-			-

FD: Functional diversity, GR: Guild richness, NA: Network asymmetry, PD: Phylogenetic diversity, PS: Precipitation seasonality, SE: Sampling effort, TS: Temperature seasonality. Σw_i: mean importance of each predictor variable measured across all models which accumulated sum higher than 0.95; AVM: standardized coefficients of the averaged model; MAM, standardized coefficients of the minimum adequate model with the lowest ΔAIC_c.

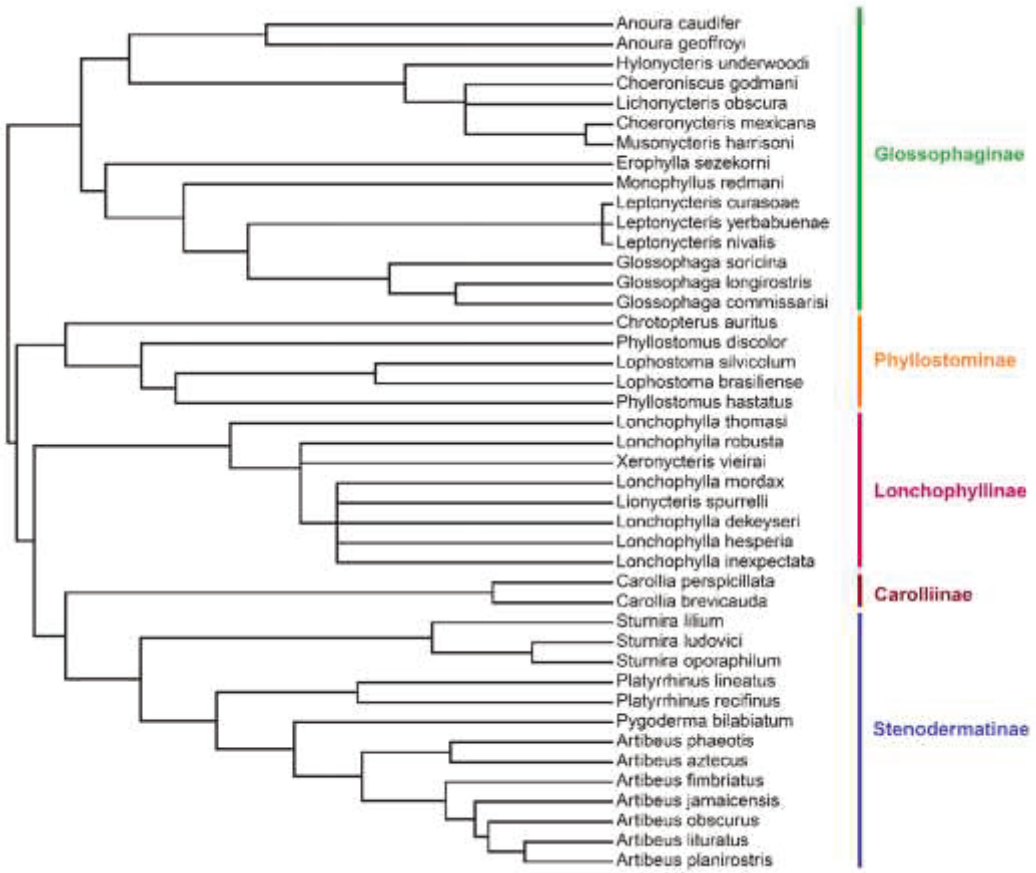

Figure S4.1 - Bat phylogeny with terminal polytomies (Based on Shi & Rabosky 2015, see methods for further information Obligatory nectar-feeding bats are included in the subfamilies Glossophaginae and Lonchophyllinae.

CONCLUSÃO GERAL

No sistema de polinização morcego-planta do Neotrópico a sobreposição de nicho (interações) das plantas é determinada pela sazonalidade da precipitação e a riqueza das plantas, sendo que existe uma menor sobreposição de nicho em comunidades mais sazonais na precipitação e com menor riqueza de plantas. Além disso, a sobreposição de nicho dos morcegos é determinada pela diversidade filogenética destes, sendo que comunidades com maior diversidade filogenética de morcegos possuem menor sobreposição de nicho. Estes resultados reforçam a influência da sazonalidade climática, riqueza de espécies e diversidade filogenética na estrutura das interações dos sistemas de polinização por vertebrados no Neotrópico. A sazonalidade climática é um fator determinante da especialização de interações para polinizadores invertebrados e para outros tipos de interação mutualística, como a dispersão de sementes. A influência da riqueza de plantas sobre as interações varia entre sistemas, segundo o grupo de polinizadores. Além disso, a diversidade filogenética é importante não só nas interações mutualísticas, mas também em redes tróficas e redes de parasito-hospedeiro. Por outro lado, existem diferenças na sobreposição de nicho dos polinizadores vertebrados no Neotrópico, sendo que as interações beija-flor-planta são mais especializadas que as interações morcego-planta. Este padrão pode derivar das diferenças na evolução e radiação de ambos os grupos de polinizadores. Porém, é necessário aprofundar nas questões relacionadas com as diferenças nos sistemas de polinização por vertebrados no Neotrópico, já que esse não era o foco principal do nosso estudo. Além disso, recomendamos a realização de mais estudos focados na interação de polinização morcego-planta, incluindo melhores identificações das plantas e morcegos encontrados nas comunidades, assim como a frequência das interações. Finalmente, é necessário continuar explorando a relação entre a sobreposição de nicho e fatores ambientais e biológicos no sistema de polinização morcego-flor, tanto do Neotrópico como do Paleotrópico.

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